ANNALS OF CARNEGIE MUSEUM
VOL. 62, NUMBER 3, PP. 245–253 30 AUGUST 1993

REDESCRIPTION OF *SPHODROSAURUS PENNSYLVANICUS* COLBERT, 1960 (REPTILIA) AND A REASSESSMENT OF ITS AFFINITIES

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ABSTRACT

Sphodrosaurus pennsylvanicus Colbert, 1960 from the Upper Triassic of Lancaster County, Pennsylvania, was originally classified as a procolophonid. The holotype and only known specimen is preserved in a hornfelsed mudstone of the Hammer Creek Formation, which may be early Norian in age. The recently prepared holotype is a natural mold of a partial skull and skeleton and was restudied using high-fidelity latex rubber casts. The alleged cranial frill comprises the posterior ends of both mandibular rami. The atlanto-occipital joint is placed well forward of the jaw articulation. The centra of the cervical and most of the dorsal vertebrae have strongly developed mid-ventral keels. *Sphodrosaurus* is clearly not a procolophonid, but it can be referred to the Diapsida on the basis of several skeletal features. Its affinities within Diapsida, however, remain unresolved, although it is probably a neodiapsid.

INTRODUCTION

Colbert (1960) described the partial skull and postcranial skeleton of a small reptile, preserved for the most part as a natural mold in a block of hornfelsed mudstone of Late Triassic age from a quarry east of Bowmansville in Lancaster County, Pennsylvania (see below). Following preliminary identification of the fossil as a specimen of *Hypsognathus fenneri* Gilmore, 1928 by the late David Dunkle (then at the United States National Museum), Colbert assigned it to the Procolophonidae, but he designated it as the holotype of a new genus and species, *Sphodrosaurus pennsylvanicus.* His assessment was subsequently accepted by Kuhn (1969) and Ivakhnenko (1979) in their systematic reviews of the Procolophonia. Baird (1986) first pointed out that *Sphodrosaurus* was not a procolophonid, and he suggested rhynchosaurine affinities instead. At his suggestion, Olsen borrowed the holotype from the North Museum of Franklin and Marshall College. He carefully removed the poorly preserved bone adhering in some parts of the natural mold in preparation for casting it using high-fidelity flexible compounds. Recently prepared latex rubber casts reveal many new details of the structure of the specimen (which previously had not been prepared) and form the basis for our redescription of *Sphodrosaurus pennsylvanicus* and reassessment of its affinities.

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Submitted 19 February 1993.

Colbert (1960) explicitly compared *Sphodrosaurus pennsylvanicus* to the only North American procolophonid then described, *Hypsognathus fenneri* Gilmore, 1928. *Hypsognathus* was originally known only from the Upper Triassic (Norian) Passaic Formation (formerly Lower Brunswick Formation) of the Newark basin of the Newark Supergroup in New Jersey (Gilmore, 1928; Colbert, 1946). Subsequently, this taxon was also recorded from the New Haven Arkose of Connecticut and the upper Wolfville Formation of Nova Scotia (Olsen, 1980; Baird, 1986). Although confident in assigning *Sphodrosaurus* to the Procolophonidae, Colbert noted that it differed from other known taxa of that group in a number of features, especially the hindlimb.

Geological Setting

The block bearing the holotype of *Sphodrosaurus pennsylvanicus* came from what was already in the mid-1950s an inactive quarry described as " . . . on the Honeybrook quadrangle, one-fourth inch above the 'B' in 'Brecknock,' Brecknock Township, Lancaster County" (Price, 1956:168). The quadrangle in this reference is that published by Bascom and Stose (1938), rather than a standard 7.5 minute United States Geological Survey quadrangle. Olsen has relocated the old quarry adjacent to the north side of Yellow Hill Road, about 200 m E of its intersection with Oaklyn Road. Latitude and longitude are approximately 40°11′45″N and 75°59′50″W. This position is about 1.4 km E of Bowmansville, Lancaster County, Pennsylvania.

In the vicinity of Bowmansville, massive intrusions of diabase plutons of Early Jurassic age have extensively altered surrounding sedimentary rocks. The old quarry is located in gray hornfelsed mudstone near one of these intrusive bodies within the Hammer Creek Formation sensu Glaeser (1963). The Hammer Creek Formation itself consists of thick sequences of brown and red conglomerate and pebbly sandstone that alternate with thinner sequences of red mudstone. The formation links the contemporaneous Passaic Formation of the Newark basin to the east with the Gettysburg Shale of the Gettysburg basin to the west. Based on an average dip of 20°, the locality is stratigraphically situated about 1.4 km above the top of the Stockton Formation and about 1.6 km above the pre-Newark contact. The exact stratigraphic position relative to the well-known sequence in the Newark basin, however, is uncertain (Fig. 1).

The mapped distribution of the mudstone sequence from which the fossil originates can be traced along strike to the northeast where it meets the Birdsboro diabase dike. Based on the mapped offset of the position of the Lockatong Formation pinch-out on the east and the boundary between the Stockton and Hammer Creek formations on the west side of the dike, the stratigraphic position of *Sphodrosaurus pennsylvanicus* should be between the upper Lockatong Formation and the Graters Member of the Passaic Formation, most likely somewhere close to member D or E–F (Fig. 1). This would place it close to the Carnian–Norian boundary, possibly early Norian (Cornet, 1977; Fig. 1).

The mudstones of the Hammer Creek Formation have not been well studied. The generally laterally persistent, thin beds (at the quarry scale) indicate a primarily lacustrine depositional environment for many of the finer-grained units. This is consistent with inferences concerning a lacustrine origin for most of the fine-grained intervals of both the contemporaneous and contiguous Passaic and Gettysburg formations (Olsen, 1986; Smoot, 1991).

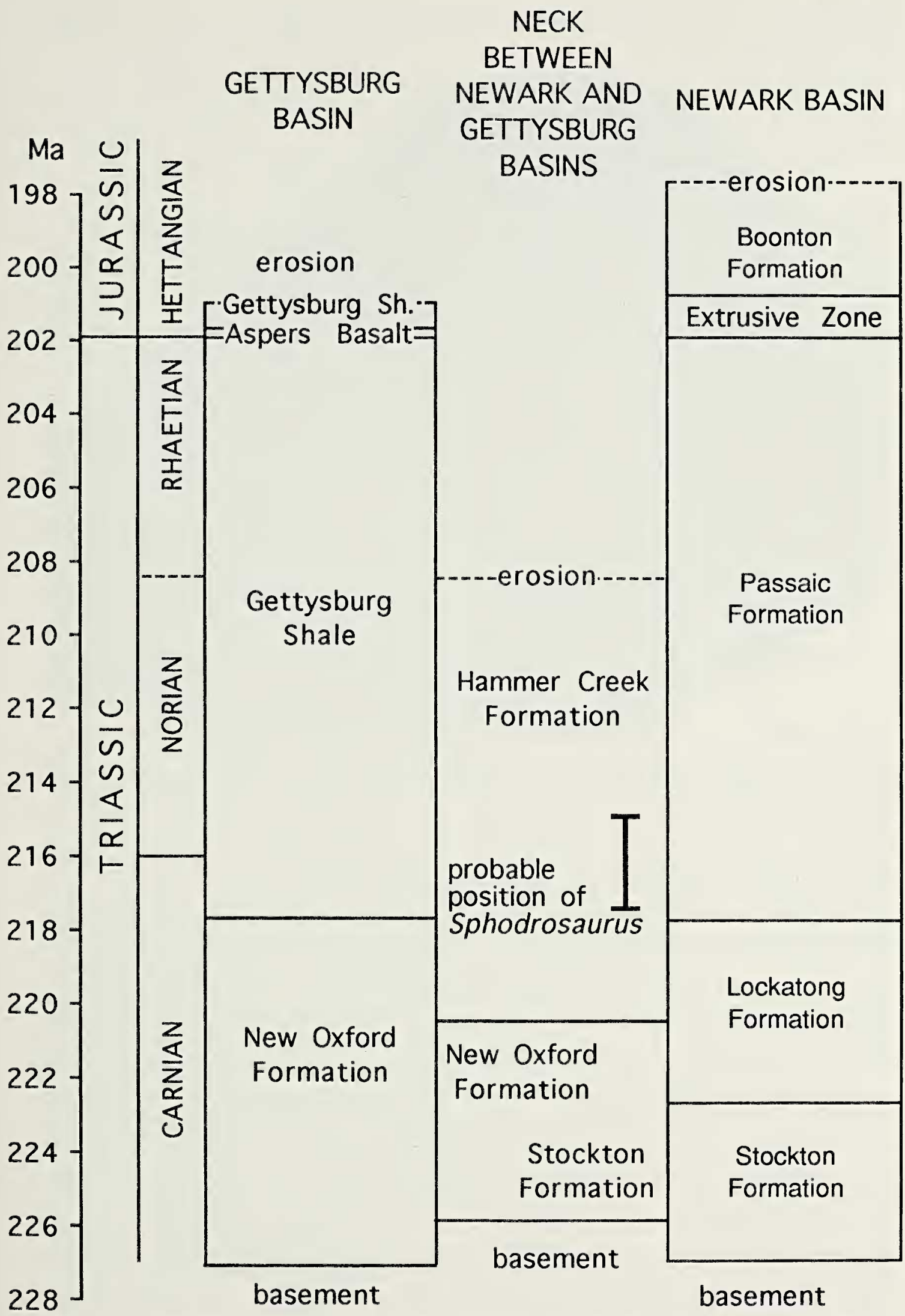

Fig. 1.—Probable stratigraphic position of the *Sphodrosaurus* horizon. Time scale and stratigraphic correlations are modified from Olsen et al. (1989).

SYSTEMATIC PALEONTOLOGY

Class Reptilia
Subclass Diapsida
Order Neodiapsida *incertae sedis*
Genus *Sphodrosaurus* Colbert, 1960

Type species.—*Sphodrosaurus pennsylvanicus* Colbert, 1960 (by monotypy).

Revised diagnosis.—Head proportionately very large. Atlanto-occipital joint apparently situated well anterior to jaw joint. External surface of posterior mandibular bones distinctively sculptured with longitudinal ridges and grooves. Centra of cervical and more anterior dorsal vertebrae with strongly developed mid-ventral keels. This combination of characters has not been found in any other known diapsid.

Sphodrosaurus pennsylvanicus Colbert, 1960

Sphodrosaurus pennsylvanicus Colbert, 1960: 2.

Holotype and only known specimen.—Franklin and Marshall College, North Museum, no. 2321, natural mold of a partial skull and postcranial skeleton exposed in ventral view (Fig. 2, 3). Found by Norman Waltz before 1956 and brought to the North Museum on 24 February 1956.

Type locality and horizon.—See above.

Age.—Late Triassic (?early Norian).

Diagnosis.—Type and only known species of genus as diagnosed above.

DESCRIPTION

The specimen is preserved as a natural mold of a largely articulated partial skeleton in ventral view. Due to natural discoloration, the impression of the skeleton is lightly colored and thus readily visible against the surrounding dark gray hornfelsed mudstone (Fig. 2). The fossil comprises the posterior region of the skull and mandible, the postcranial axial skeleton back to the sacral region, gastralia, parts of the pectoral girdle and both forelimbs, the left pubis and right pelvic bones, and most of the right hindlimb (Fig. 3).

Skull and mandible.—Colbert (1960) correctly noted the unusually large size of the skull relative to the body. Only the rather wide posterior region of the skull is preserved. A "long expanse of sculptured bone on each side" was interpreted by Colbert (1960:8) as representing "the lower damaged edges of the quadratojugals, squamosals, and tabulars." He regarded them as part of a frill along the back of the skull over the cervical region. Preparation revealed that these structures actually represent the posterior ends of the two mandibular rami (Fig. 3, mr). The ventral margin of each ramus forms a sharp, somewhat inturned edge. The external surface is irregularly sculptured with longitudinal ridges and grooves. The truncated posterior end of each jaw ramus comprises articular and prearticular; the suture between these bones is only visible in posterior view. There is no distinct retroarticular process. In the basicranial region, Colbert (1960:9) noted the presence of bone, which he interpreted as "in part the opisthotic, with perhaps other elements (perhaps the proötic) joining it" and which he labelled as the right prootic in his illustration (Colbert, 1960:fig. 6). We identify this bone as the right pterygoid (Fig. 3, pt). The transverse process of this element is visible along the top edge of the block, and its quadrate flange can be traced posterolaterally, where it probably contacts the quadrate. A portion of the left pterygoid is also exposed.

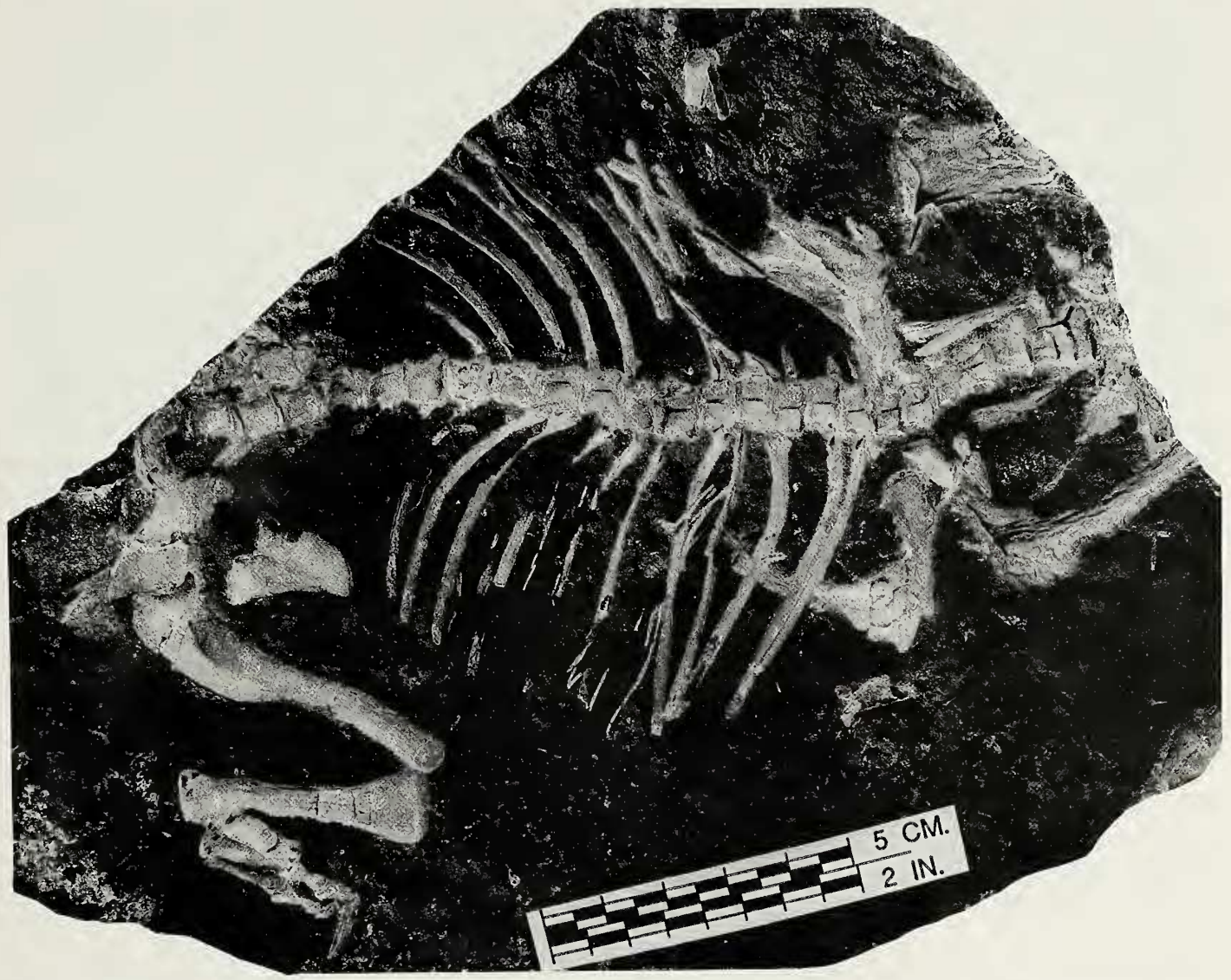

Fig. 2.—Natural mold of the partial skeleton of *Sphodrosaurus pennsylvanicus* Colbert, 1960 (North Museum, Franklin and Marshall College, no. 2321, holotype) after completed preparation.

Most of the basicranial region is not preserved. The atlanto-occipital joint, however, appears to be placed well forward of the jaw articulation. Although some postmortem displacement of the mandible posteriorly cannot be entirely ruled out, it seems that the quadrate flange of the pterygoid and the pterygoid flange of the quadrate have not been displaced.

Vertebrae and ribs.—Colbert (1960:9) reported 26 vertebrae in a more or less articulated series between the skull and pelvis, of which 25 are said to be presacrals. After preparation, we count only a total of 22 post-atlantal centra, all of which are exposed in ventral view (contra Colbert). Details of the atlanto-occipital region are unclear. Colbert noted a "large broad spine" on the axis, which he interpreted as the neural spine of that vertebra but which actually represents a separate piece of bone of uncertain identity. Intercentra are absent. Starting at the axis, the anterior 16 vertebral centra possess strongly developed longitudinal, mid-ventral keels, which begin to diminish at the 19th vertebra. The amphicoelous centra bear prominent, raised parapophyseal facets anteriorly. Their anterior and posterior articular ends have distinct rims. The centra of the post-axial cervical vertebrae are shorter than those of the dorsals. The centrum of the last preserved vertebra probably represents a sacral, as suggested by Colbert, and there is an apparent sacral rib adjacent to it on the right side.

Several long cervical ribs (Fig. 3, cr) extend parallel to the second to fifth vertebra

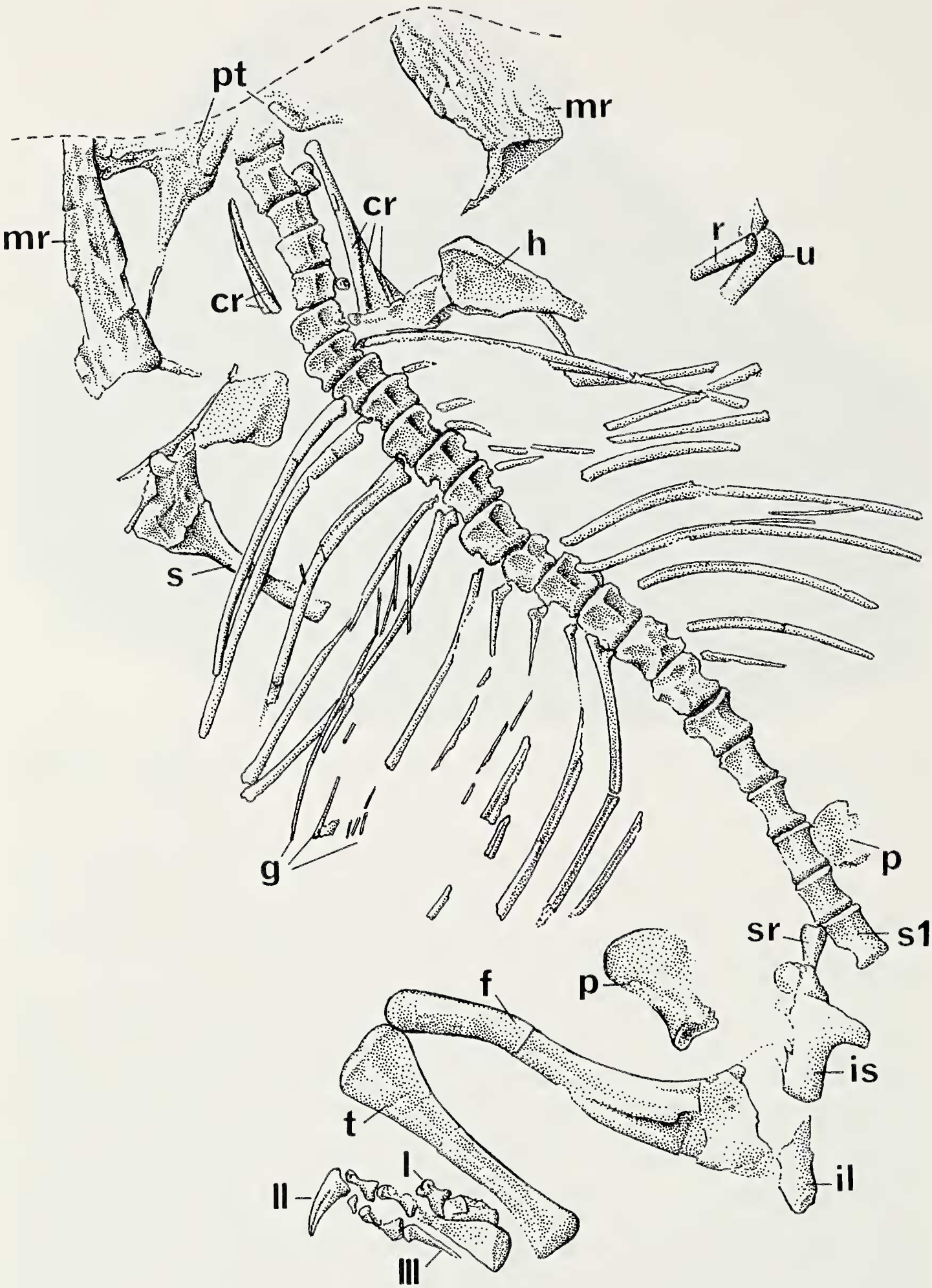

Fig. 3.—*Sphodrosaurus pennsylvanicus* Colbert, 1960, drawing based on a latex peel of the holotype. Abbreviations: cr, cervical ribs; f, femur; g, gastralia; h, humerus; il, ilium; is, ischium; mr, mandibular ramus; p, pubis; pt, pterygoid; r, radius; s, scapula; s1, sacral vertebra 1; sr, sacral rib; t, tibia; u, ulna; I–III, pedal digits I–III. Scale bar equals 2 cm.

on each side; their anterior ends are not visible. The long, slender dorsal ribs are only slightly curved, indicating a broad trunk region. The rib-heads are not clearly exposed, and it is impossible to ascertain from the casts whether they are dichocephalous or holocephalous. Fragments of very slender, rod-like gastralia (Fig. 3, g) are preserved in several places of the mid-trunk region. There is no evidence of dermal armor.

Pectoral girdle and forelimb.—The scapula (Fig. 3, s) has a tall, slightly recurved, and apparently slender blade, which is exposed between several ribs on the right side. Details of the base of the scapula and the coracoid region are obscured by crushing. The humerus, partially exposed on both sides but most clearly visible on the left side (Fig. 3, h), has a broad proximal end merging into a narrow shaft; its distal portion is buried in the matrix on either side. Radius (r) and ulna (u) are only documented by the associated distal portions of the left elements (Fig. 3). The distal end of the ulna has a convex surface for articulation with the carpus.

Pelvic girdle and hindlimb.—The right ilium, right ischium, and both pubes are preserved (Fig. 3). The ilium (il) preserves few unambiguous details. The ischium (is) and pubis (p) are both large, plate-like bones. The right hindlimb is sharply flexed at the hip, knee, and ankle. Colbert correctly noted that it is long, in its extended position subequal in length to the entire presacral vertebral column. The femur (Fig. 3, f), exposed in posterior view, is approximately 57 mm long and equal in length to about nine posterior dorsal centra. Its fairly slender shaft is sigmoidally curved. The damaged proximal head of the femur is large and inturned dorsomedially. The medial distal condyle projects ventrally. A prominent ventral ridge is developed on the proximal half of the femur. The slightly crushed tibia (Fig. 3, ti), exposed in medial view, is robust and distinctly shorter than the femur (39 mm vs. c. 57 mm).

No unambiguous tarsal elements are preserved. Parts of three digits of the right pes are exposed in ventromedial view (Fig. 3, I–III). The first metatarsal, which overlaps the second proximally, is flattened, roughly quadrangular, and 8.5 mm long. Its broad distal ginglymus is set at an angle of about 50° to the shaft, indicating that the hallux diverged medially. A stout phalanx articulates with metatarsal I; ventral to it there is a trace of an ungual that is buried deeper in the rock. Metatarsal II is concealed medially and distally, the exposed portion being 15 mm long; it is broad proximally and rapidly narrows to a slender waist more distally. The second pedal digit has three phalanges including a sharply pointed ungual that is long and straight and bears a distinct lateral groove for the horny sheath of the claw. The lateral edge of metatarsal III is exposed for a length of about 13 mm but its proximal end is concealed. Articulating in sequence with it are a long first phalanx and the proximal end of the second. The fourth and fifth digits are not exposed. The pes was probably more or less equal in length (in its fully extended position) to the tibia.

AFFINITIES OF *SPHODROSAURUS PENNSYLVANICUS*

The mode of preservation of the holotype and only known specimen of *Sphodrosaurus pennsylvanicus* leaves very few anatomical features for assessing its phylogenetic position. We found no derived characters to support reference of this taxon to the Procolophonidae. Colbert (1960:17–18) cited "size, the obviously large skull, the extension of the back of the skull in a sort of frill over the cervical region, the evidently broad vertebral neural arches (as indicated by the separation of the heads of the ribs), and the holocephalous, flaring ribs" in support of procolophonid affinities. Aside from the phylogenetically uninformative size crite-

rion, we have demonstrated above that the alleged frill is based on what are actually the posterior ends of the mandibular rami. The inferred width of the neural arches is of questionable diagnostic value. The nature of the proximal articular end of the trunk ribs is unclear, but holocephalous ribs are also present in most diapsid reptiles (Laurin, 1991).

As Colbert recognized, several features clearly distinguish *Sphodrosaurus* from known procolophonid taxa. These characters indicate diapsid affinities. The rather slender femur with its sigmoidally curved shaft is the only observable character to support reference of *Sphodrosaurus* to the Neodiapsida as diagnosed by Benton (1985). Although the distal portion of the left humerus is not completely exposed, it is apparent from the proportions of the left forelimb that it was distinctly shorter than the femur, much as in neodiapsids (Laurin, 1991). The strongly developed mid-ventral keeling on the cervical and more anterior dorsal centra of *Sphodrosaurus* also indicates diapsid affinities (although at least the centra of the more anterior dorsal vertebrae in *Hypsognathus fenneri* also bear mid-ventral keels; Sues, personal observation), but most diapsid reptiles except *Araeoscelis* (Laurin, 1991) show less pronounced keeling. The phylogenetic significance of the absence of a retroarticular process is uncertain (*see* Laurin, 1991).

Baird's (1986) reference of *Sphodrosaurus* to the Rhynchosaurinae was based on the position of the atlanto-occipital joint well forward of the jaw joint. This condition is unlike that found in the Procolophonidae (Ivakhnenko, 1979). It is present not only in rhynchosaurine rhynchosaurs (Benton, 1990), but also in various other Triassic archosauromorph reptiles such as *Erythrosuchus* (Huene, 1911) and *Proterosuchus* (Broili and Schröder, 1934; Cruickshank, 1972). The holotype of *S. pennsylvanicus* preserves none of the other features considered diagnostic for Rhynchosauria by Benton (1990), and we found no derived characters in support of reference to the Archosauromorpha (as diagnosed by Benton, 1985) in general.

Possibly diagnostic features of *Sphodrosaurus pennsylvanicus* include the proportionately very large head, the well-developed, distinctive sculpturing composed of longitudinal ridges and grooves on the external aspect of (at least) the posterior mandibular bones, the strongly developed mid-ventral keeling of the cervical and more anterior dorsal centra, and the great width of the trunk region. *Sphodrosaurus* does not closely resemble any other known early Mesozoic diapsid and represents one of a growing number of tetrapods from the Triassic portion of the Newark Supergroup of eastern North America that defy placement in currently recognized higher taxa. Additional material is clearly needed to clarify the affinities of this distinctive little reptile.

ACKNOWLEDGMENTS

We thank R. M. Busch (North Museum, Franklin and Marshall College) for making the specimen available for study, and P. A. Kroehler (National Museum of Natural History) for preparing the casts. V. Krantz (National Museum of Natural History) took the photograph used in Fig. 2. J. Mulock (Toronto) prepared the drawing for Fig. 3. We are indebted to D. S Berman and J. M. Clark for their helpful comments on the manuscript.

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